Antagonistic coevolution between multiple quantitative traits: matching interactions can be subsets of difference interactions

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ABSTRACT

Coevolution is one of major drivers of complex dynamics in population ecology. Historically, antagonistic coevolution in victim-exploiter systems has been a topic of special interest, and involves traits with various genetic architectures (e.g., the number of genes involved) and effects on interactions. For example, exploiters may need to have traits that "match" those of victims for successful exploitation (i.e., a matching interaction), or traits that exceed those of victims (i.e., a difference interaction). Different models exist which are appropriate for different types of traits, including Mendelian (discrete) and quantitative (continuous) traits. For models with multiple Mendelian traits, recent studies have shown that antagonistic coevolution with matching interactions can be a subset of coevolution with multiple difference interactions. Here we generalize their findings to quantitative traits and show, analogously, that the widely used "bidirectional" framework for matching interactions can be a subset of a multidimensional

"unidirectional" framework for difference interactions. While previous studies have used the dichotomy between bidirectional and unidirectional frameworks to explore coevolutionary dynamics, we suggest that exploring multidimensional trait space is important to examine the generality of results obtained from one-dimensional traits.

Keywords: bidirectional axis of vulnerability, fluctuating selection, gene-for-gene, matching allele, unidirectional axis of vulnerability

INTRODUCTION

Theories developed from specific models are initially only as general as their underlying models, until they are shown to hold in other modeling frameworks. Hence, it is critical to compare results from a variety of modeling frameworks to test their generality. Antagonistic coevolution in victim-exploiter systems (e.g., prey-predator or host-pathogen systems) has been intensively studied theoretically (Abrams 2000, Nuismer 2017). It is thought to be a major driver for the emergence and maintenance of biodiversity (Thompson 2005) and feedbacks between interacting species can create complex ecological (e.g., Cortez and Weitz 2014) and evolutionary (e.g., Dercole et al. 2010) dynamics. Historically, various coevolution models with differing genetic architectures (e.g., the number of genes involved) and interspecific interactions (e.g., a "matching" vs. a "difference" interactions: see below) have been proposed and analyzed (Nuismer 2017). To account for genetic architecture, some researchers have considered coevolution with a few major genes that interact and produce a discrete phenotype (Mendelian trait-based models, or hereafter Mendelian models). On the other hand, quantitative trait-based models (hereafter quantitative models) assume the genetic architecture consists of many genes of small effect and produce continuous phenotypes.

Here we highlight the connection between Mendelian and quantitative models and then clarify the relationships between existing modeling frameworks for quantitative traits. We begin by reviewing the different modeling frameworks for Mendelian traits. We then draw analogies between Mendelian and quantitative models. The analogies suggest that the bidirectional framework, in which exploitation is more successful when traits "match" (i.e., the matching interaction), can be a subset of the unidirectional framework, in which exploitation is more

51 successful when traits differ (i.e., the difference interaction), in multidimensional quantitative
52 models. Finally, as a proof of concept, we give an example of a victim-exploiter system where
53 there are two pairs of unidirectional traits that can be seen as two one-dimensional bidirectional
54 traits.
55
56 **BACKGROUND**

57 Historically, in Mendelian models, two major interactions were often assumed and
58 contrasted: the matching allele (MA) framework, in which exploitation is successful when traits
59 match (e.g., Grosberg and Hart 2000) (Fig. 1A), and the gene-for-gene (GFG) framework, in
60 which a generalist exploiter can exploit a range of victim genotypes, but pays a cost for
61 generalism (Flor 1956) (Fig. 1B). Researchers have investigated the relative importance and
62 relationships of the two interactions (e.g., Parker 1994, Frank 1996, Agrawal and Lively 2002).
63 Recently, Ashby and Boots (2017) found that, in multidimensional Mendelian (multilocus)
64 models, the MA framework can be a subset of the GFG framework (Fig. 2A). To illustrate,
65 consider a simple GFG model with haploid victims and exploiters with two loci with two alleles
66 each, labelled 1 and 0. The alleles 1 and 0 indicate the presence and absence, respectively, of an
67 exploitation or defense trait (Fig 2A). In this model, the exploiter genotype 11 can exploit all
68 victim genotypes (black square in Fig. 2A), but the exploiter genotype 00 cannot exploit the
69 victim 11 (white square in Fig. 2A) and the exploitation is weak for the victim 01 and 10 (gray
70 square in Fig. 2A). If having both exploiter or defense alleles is too costly, victims and exploiters
71 may evolve to have only one of the two possible alleles, i.e., either the genotype 01 or 10 (dashed

72 white region in Fig 2A). Then the type of interaction effectively reduces to a MA interaction: the
73 exploiter genotype 01 (10) is more successful at exploiting its matching counter victim genotype
74 01 (10) as in Fig 1A.

75 Indeed, by investigating a multilocus GFG model, Ashby and Boots (2017) found that
76 when investing an intermediate number of alleles is optimal due to the costs of having
77 defense/exploitation alleles, victim/exploiter genotypes alternate between various subsets of
78 defense/exploitation alleles, but the total number of alleles stays constant. Hence, the
79 multidimensional GFG framework effectively becomes the MA framework (Fig. 2A). Ashby and
80 Boots (2017) refer to these alterations as "within-range cycles." In contrast, in other scenarios,
81 the total number of defense/exploitation alleles also fluctuates, which they called "between-range
82 cycles," leading Ashby and Boots (2017) to conclude that the MA framework is a subset of the
83 GFG framework in multidimensional Mendelian models.

84 As with Mendelian models, quantitative models have assumed an apparent dichotomy
85 between two frameworks (Abrams 2000, McPeek 2017): the bidirectional trait framework, in
86 which exploitation is increasingly more successful with the extent that trait values of exploiters
87 match those of victims (Fig. 1C), and the unidirectional trait framework, in which exploitation is
88 increasingly more successful with the extent that trait values of exploiters exceed those of victims
89 (Fig. 1D). They are also known as the matching and difference trait cases (Gilman et al. 2012).
90 The bidirectional framework is appropriate, for example, when an exploiter can best exploit a
91 victim with body size or color within a certain range. One example is coevolution between the
92 African tawny-flanked prinia and its brood parasite, the cuckoo finch, in which the parasite varies

its egg color to match that of the victim (Spottiswoode and Stevens 2012). On the other hand, the unidirectional framework is appropriate when exploitation success is determined by speed vs. speed, strength vs. armor, or toxicity vs. resistance. For example, garter snakes evolve stronger resistance to rough-skinned newt toxicity in areas where newts are more toxic (Brodie III and Brodie Jr 1990). Previous theoretical studies on coevolution have assumed bidirectional traits (Brown and Vincent 1992, Marrow et al. 1992, Dieckmann et al. 1995, Gavrilets 1997, Khibnik and Kondrashov 1997, Nuismer et al. 2005, Kopp and Gavrilets 2006, Calcagno et al. 2010, Dercole et al. 2010, Mougi 2012, Yamamichi and Ellner 2016, Fleischer et al. 2018), unidirectional traits (Saloniemi 1993, Frank 1994, Sasaki and Godfray 1999, Nuismer et al. 2007, Mougi and Iwasa 2010, Mougi and Iwasa 2011, Tien and Ellner 2012, Northfield and Ives 2013, Cortez and Weitz 2014, Yamamichi and Miner 2015, van Velzen and Gaedke 2017), or compared both of them (Abrams and Matsuda 1997, Gilman et al. 2012, Boots et al. 2014) and obtained various outcomes.

In the bidirectional framework, exploitation success is typically a unimodal function of the trait difference, and is often modeled as a Gaussian: $\exp[-(x-y)^2]$, where x and y are traits of victims and exploiters, respectively (Fig. 1C) (e.g., Gavrilets 1997, Khibnik and Kondrashov 1997, Nuismer et al. 2005, Mougi 2012). On the other hand, in the unidirectional framework, exploitation success is often modeled as a sigmoidal function of the trait difference: $1/[1 + \exp(x - y)]$ (Fig. 1D) (e.g., Nuismer et al. 2007, Mougi and Iwasa 2010, van Velzen and Gaedke 2017). In this framework, it is always advantageous for both species to increase the trait values for better exploitation/defense (McPeek 2017). Empirical evidence suggests that there is an energetic

trade-off to exploitation and defense and hence, most models of unidirectional traits assume there is a cost associated with each trait, which prevents runaway evolution. For example, Brodie III and Brodie Jr (1999) found a cost of resistance in garter snakes; those resistant to newt toxin have slower sprinting speeds. Note that the above functions are not the only ways to model exploitation success in the bidirectional and unidirectional frameworks, and there are other functional forms that represent the same type of interactions.

Here, by drawing analogies between the Mendelian trait and quantitative trait frameworks (Fig. 1), we further extend the generalization of Ashby and Boots (2017) and demonstrate that the bidirectional framework can be a subset of the unidirectional framework in multidimensional quantitative models.

AN EXAMPLE

We develop a two-dimensional quantitative model with unidirectional interactions (Fig. 2B) to demonstrate that an effectively bidirectional interaction can emerge from a multidimensional unidirectional framework. We assume that victims and exploiters each have two quantitative traits. We let x_i be the value of victim trait i (= 1, 2) and assume greater values allow for defense against trait i of the exploiter. We let y_i be the value of exploiter trait i and assume greater values allow for more exploitation. Each trait is associated with a cost that decreases individual fitness with greater trait values. The difference between the exploiter trait and the corresponding victim trait, $y_i - x_i$, affects exploitation success (Fig. 2B), which is expressed by a sigmoid function (Fig. 1D). In addition, we add stabilizing selection as in

Gavrilets (1997) to prevent runaway evolution to infinite trait values, which can occur in quantitative models but not in Mendelian models. It is also possible to assume a finite range of trait values instead of stabilizing selection, and it results in the similar dynamics (results not shown).

We assume that fitness of victims and exploiters are, respectively,

$$
\begin{aligned}
m_V &= C_V \exp\left\{-\beta_V \prod_i \frac{1}{1+\exp\left[\sigma_V\left(x_i - y_i\right)\right]}\right\}, \\
m_E &= C_E \exp\left\{\beta_E \prod_i \frac{1}{1+\exp\left[\sigma_E\left(x_i - y_i\right)\right]}\right\},
\end{aligned}
\tag{1}
$$

where β_V and β_E are the effects of successful exploitation on victim and exploiter fitness, respectively, and σ_V and σ_E determine the sensitivity of exploitation success to the trait difference. Here C_V and C_E represent costs of defense and exploitation for victims and exploiters, respectively, and they are decreasing functions of the sum of the two traits values (i.e., lower values of C_V and C_E represent higher costs). Following Ashby and Boots (2017), we employ the functions:

$$
\begin{aligned}
C_V &= \left[1 - c_V^1 \frac{1-\exp\left(c_V^2 \sum_i x_i\right)}{1-\exp\left(c_V^2\right)}\right] \exp\left[-c_V^3 \sum_i \left(x_i - x_{i0}\right)^2\right], \\
C_E &= 1 - c_E^1 \frac{1-\exp\left(c_E^2 \sum_i y_i\right)}{1-\exp\left(c_E^2\right)},
\end{aligned}
\tag{2}
$$

where parameters c_V^1, c_V^2, c_E^1, and c_E^2 determine the shape of the functions. We introduce stabilizing selection toward an optimum trait for victims, $(x_1, x_2) = (x_{10}, x_{20})$, where c_V^3 determines the strength of stabilizing selection. Then coevolutionary dynamics are described by four ordinary differential equations,

$$\begin{aligned} \frac{dx_i}{dt} &= v_V^i \frac{\partial m_V}{\partial x_i}, \\ \frac{dy_i}{dt} &= v_E^i \frac{\partial m_E}{\partial y_i}, \end{aligned} \qquad (i = 1, 2) \qquad (3)$$

where v_j^i ($i = 1, 2$ and $j = V, E$) represents additive genetic variance and partial derivatives represent fitness gradients (Abrams et al. 1993). Notice that each species traits evolve in the direction of increasing fitness.

By numerically solving the model, we find that the two-dimensional unidirectional model can be effectively a one-dimensional bidirectional model. In these cases, because of the shape of the functions (2) representing costs of defense/exploitation, an intermediate level of investment is optimal. This makes the two-dimensional trait dynamics to reduce down to a one-dimensional dynamics. When exploiter evolution is faster than victim evolution, the optimum trait value of stabilizing selection, (x_{10}, x_{20}), is stable. In this equilibrium, there is disruptive selection for victim traits (i.e., fitness minimum: vectors in Figs. 3B, E are distracted from the equilibrium (0.2, 0.2)) and stabilizing selection for exploiter traits (i.e., fitness maximum: vectors in Figs. 3C, F are attracted to the equilibrium), which is consistent with the

171 bidirectional interaction (Abrams and Matsuda 1997, Gavrilets 1997).

172 When victim evolution is faster than exploiter evolution (e.g., $v_V^i = 0.3$ and $v_E^i = 0.1$),
173 the trait dynamics fluctuate but are constrained to regions in which the total investments are
174 nearly constant and the two traits for each species show antiphase cycles (Figs. 3A-C). In other
175 cases (e.g., when victim evolution is faster: $v_V^i = 1$), the total investments fluctuate (Figs. 3D-F).
176 Hence, the unidirectional interactions can produce both coevolutionary cycles with nearly
177 constant investments (similar to "within-range cycles" of Ashby and Boots (2017)) as well as
178 cycles with fluctuating investments (similar to "between-range cycles" of Ashby and Boots
179 (2017)), demonstrating that the bidirectional interaction can be a subset of the unidirectional
180 interaction. This generalizes Ashby and Boots (2017)'s idea from Mendelian models to
181 quantitative models.

182

183 **DISCUSSION**

184 Victim-exploiter interactions are among the most fundamental type of ecological
185 interactions. In addition to their importance in ecological communities, these interactions are
186 widely recognized for playing an important role in ecological dynamics (e.g., extinction and
187 predator-prey cycles: Northfield and Ives (2013), Cortez and Weitz (2014)) and evolutionary
188 dynamics (e.g., sex, recombination, and epistasis: Otto and Lenormand (2002)), because each
189 species needs to continue to adapt to new selection pressures by the other species. Due to its
190 importance, many modeling frameworks have been proposed to investigate the dynamics of
191 coevolution between a victim and its exploiter, capturing various aspects of the traits

192 involved (Nuismer 2017).

193 In this work, we highlight the relationship between two particular modeling
194 frameworks of quantitative traits in victim-exploiter coevolution. In particular, the bidirectional
195 framework, in which traits between a victim and exploiter must "match" in some sense for
196 successful interactions (Fig. 1C), can be a subset of a multidimensional unidirectional trait
197 framework, in which each trait confers an advantage in the victim-exploiter interaction but is
198 associated with some cost (Figs. 1D, 2B). We extend previous models of coevolution to
199 demonstrate how effectively bidirectional traits can be generated from unidirectional traits as a
200 proof of concept (rather than a thorough investigation of the dynamics: Fig. 3).

201 However, for Mendelian (discrete) traits, the distinction between within- and
202 between-range cycles is clear: within-range involves changes in the type of investment but not
203 total investment, while between-range involves changes in total investment (Ashby and Boots
204 2017). On the other hand, due to the continuous nature of quantitative traits, cycles always
205 simultaneously involve at least some fluctuations in both type and total investment (Fig. 3).
206 Hence, they are not as easily distinguished, suggesting a need for a more nuanced classification
207 of coevolutionary cycles.

208 Previous work has suggested that bidirectional traits are more likely to lead to
209 coevolutionary cycling of traits than unidirectional interactions (Abrams 2000, McPeek 2017). In
210 comparing quantitative models with a one-dimensional trait, for example, McPeek (2017) found
211 cycles are observed in a smaller area of parameter space with unidirectional traits compared to
212 bidirectional traits. Furthermore, the underlying mechanism of cycles differs in the two

frameworks. In the bidirectional framework, cycles consist of the exploiter tracking victim traits and the victim escaping from exploiter traits (i.e., fluctuating selection between equally specific defense/exploitation traits). In the unidirectional framework, cycles consist of the victim and exploiter investing more energy in their traits for better defense/exploitation, and then abandoning their defense/exploitation because at some point they are too costly to maintain (i.e., fluctuating selection between strong and weak defense/exploitation traits). Even when empirical researchers are focusing on a single trait with the unidirectional interaction, the system may have another unidirectional trait that can affect exploitation success. In such a case, coevolutionary dynamics can be driven by the bidirectional interaction, which can cause cyclic dynamics more easily (McPeek 2017).

In spite of recent interest in coevolution in multidimensional trait space (e.g., Gilman et al. 2012, Débarre et al. 2014, Doebeli and Ispolatov 2017), the subset relation of the bidirectional and unidirectional frameworks has not been well recognized. For example, in their study on evolutionary escape, Gilman et al. (2012) contrasted coevolutionary dynamics with bidirectional and unidirectional interactions in multidimensional trait space but did not find a significant difference between them (see Fig. 1 of Gilman et al. (2012)). Our generalization offers a potential explanation for this previous work, as coevolutionary dynamics with bidirectional interactions can be a subset of unidirectional interactions in multidimensional quantitative models.

This work was inspired by the recent work of Ashby and Boots (2017), who showed an analogous relationship for two Mendelian trait models of coevolution. Here, we draw out the parallels between two Mendelian (single-locus) trait frameworks and two quantitative trait

frameworks. Namely, we highlight that the matching allele (MA) framework is a Mendelian analog of the bidirectional framework, and the gene-for-gene (GFG) framework is a Mendelian analog of the unidirectional framework (Fig. 1). While these frameworks are valuable, many traits important to victim-exploiter interactions may actually lie somewhere in the middle of these two extremes; they may be determined by many (but not infinite number of) loci. It is still not well understood how coevolutionary dynamics differ between when traits are governed by a single locus, multi-locus (with linkage disequilibrium and epistasis), and effectively infinite loci (as assumed in classical quantitative genetics). While there have been a handful of papers to investigate this question in specific scenarios, further investigation is need for a general understanding.

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346 **FIGURE LEGENDS**

347 **Figure 1.** Interaction frameworks and genetic architectures in coevolution models. A: Matching
348 allele (MA) is a matching interaction in Mendelian traits. B: Gene-for-gene (GFG) is a difference
349 interaction in Mendelian traits. Here victims and exploiters are haploid and their genotypes are
350 represented by 1 and 0 at a particular locus, and they indicate the presence and absence,
351 respectively, of defense/exploitation alleles. Dark shading indicates greater exploitation success.
352 C: Bidirectional interaction is a matching interaction in quantitative traits. Exploitation success is
353 maximized when the trait difference is zero. D: Unidirectional interaction is a difference
354 interaction in quantitative traits. Exploitation success is increased by larger exploiter trait values
355 and by smaller victim trait values.

356

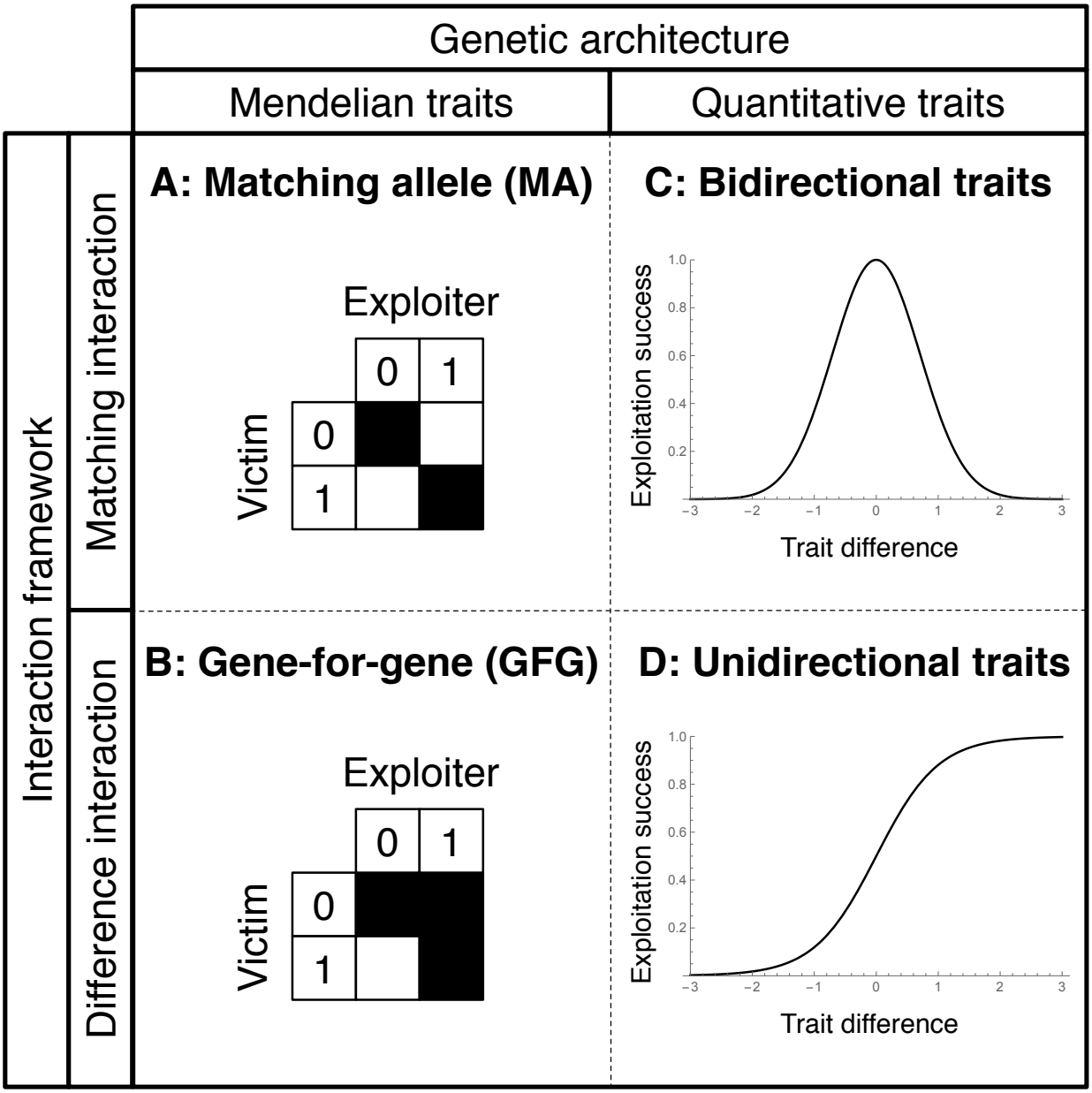
357 **Figure 2.** A: An example of exploitation matrix of in a Mendelian GFG model with two loci
358 (Ashby and Boots 2017). The region surrounded by a dashed white line shows that the MA
359 framework is a subset of the GFG framework. Victims and exploiters are haploid and their
360 genotypes are represented by 1 and 0 at a locus, and they indicate the presence and absence,
361 respectively, of defense/exploitation alleles. Darker shading indicates greater exploitation success
362 and arrows indicate greater costs. B: Exploitation success as a function of both trait differences
363 between exploiters and victims in a quantitative unidirectional (difference) model with two traits.

364

365 **Figure 3.** Coevolutionary dynamics of two quantitative traits with unidirectional interactions.
366 Numerical solutions of our model when victim evolution is relatively slow ($v_V^i = 0.3$: A-C) and

relatively fast ($v_V^i = 1$: D-F) are shown. A, D. Time-series of the four traits (top panel) and the functions (2) representing costs of defense/exploitation (note that lower values indicate higher costs: bottom panel). B, C, E, and F: Fitness landscapes and coevolutionary cycles of victims (B, E) and exploiters (C, F). Contour plots and vector fields of fitness of victim traits (B, E) when exploiter traits are at the optimal trait value of stabilizing selection ($y_1 = y_2 = 0.2$) and of exploiter traits (C, F) when victim traits are at the optimal trait value of stabilizing selection ($x_1 = x_2 = 0.2$). Other parameter values are $c_V^1 = c_E^1 = 0.2$, $c_V^2 = c_E^2 = 3$, $c_V^3 = 0.01$, $x_{10} = x_{20} = 0.2$, $\beta_V = \beta_E = 1$, $\sigma_V = \sigma_E = 0.85$, and $v_E^i = 0.1$.

Figure 1.


Genetic architecture
Mendelian traits
Quantitative traits
Interaction framework
Matching interaction
Difference interaction
A: Matching allele (MA)
Exploiter
Victim
0
1
0
1
C: Bidirectional traits
Exploitation success
Trait difference
B: Gene-for-gene (GFG)
Exploiter
Victim
0
1
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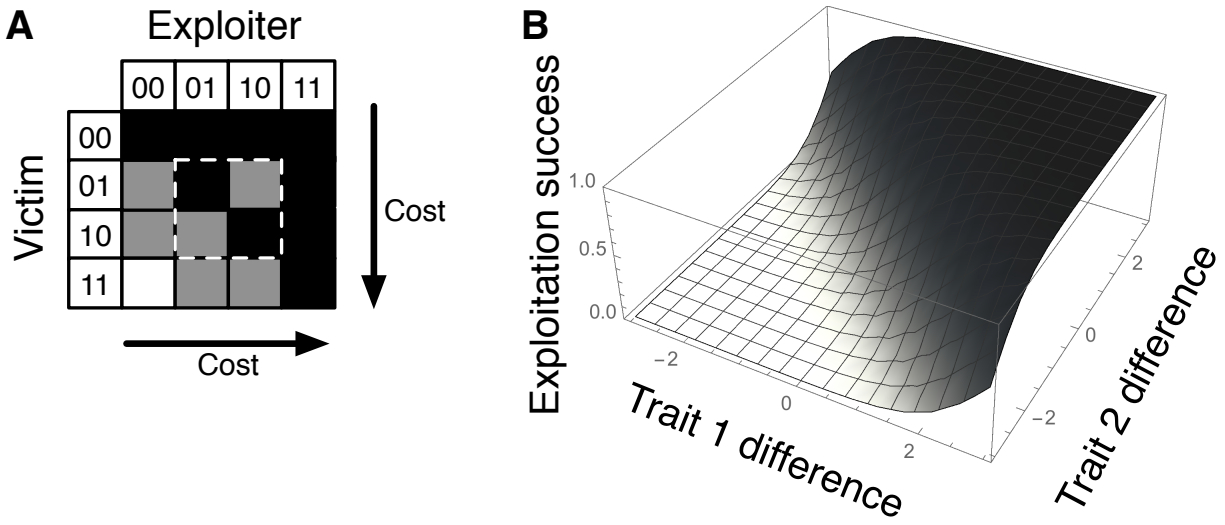
D: Unidirectional traits
Exploitation success
Trait difference

Figure 2.


A
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1.0
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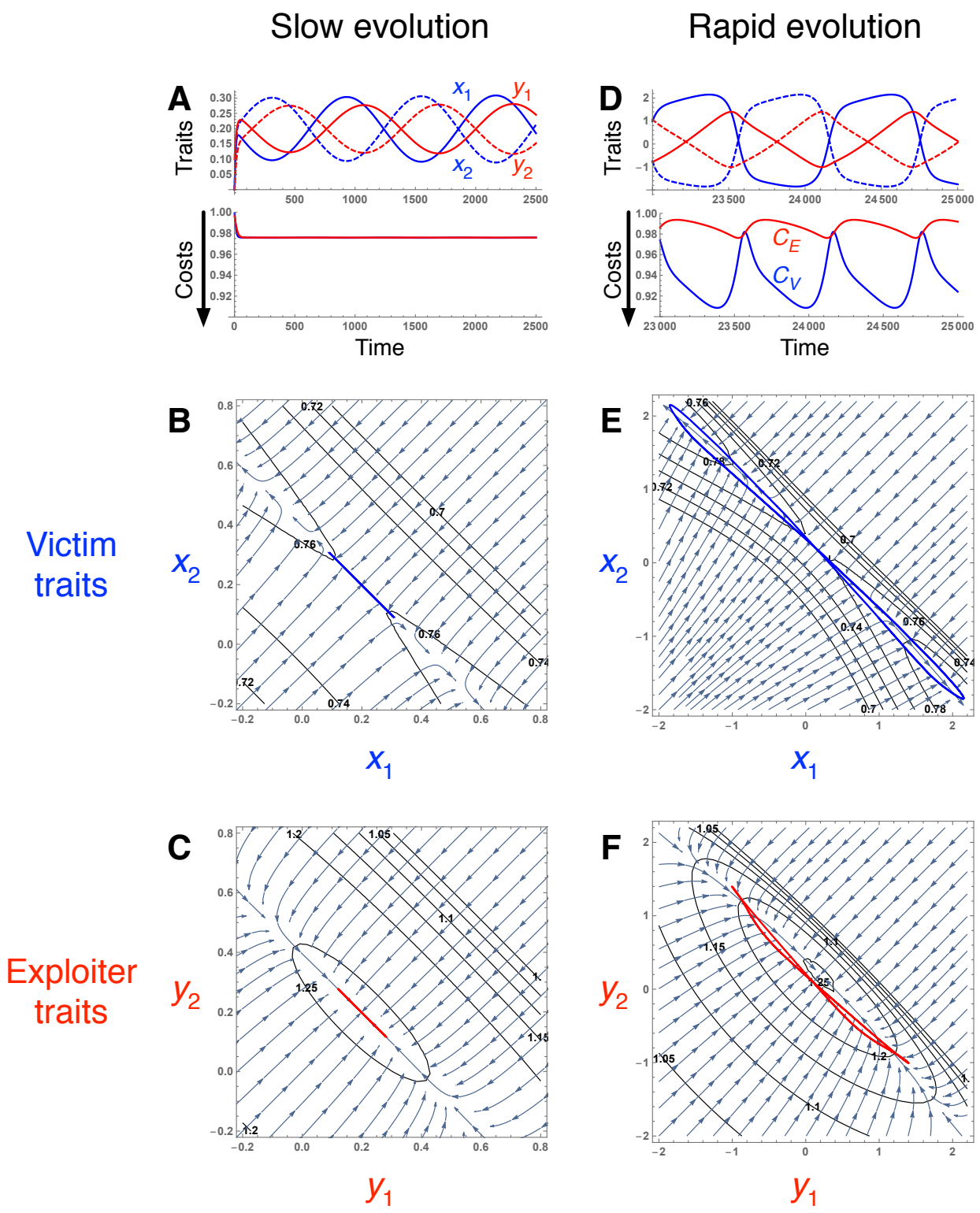
−2
Trait 2 difference

Figure 3.


Slow evolution
Rapid evolution
A
D
Traits
Costs
Time
x_1
x_2
y_1
y_2
C_E
C_V
B
E
C
F
Victim traits
Exploiter traits